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Dear Editor,

I am pleased to submit the original manuscript "An Algorithm for the von Bertalanffy Seasonal Cessation in Growth Function of Pauly et al. (1992)" as a Technical Note to *Fisheries Research*. This manuscript provides an algorithm that makes the growth function of Pauly et al. (1992) available to all fisheries scientists with software that performs simple nonlinear modelling. Pauly et al. (1992) originally provided closed-source software to perform these analyses, but that software (and its source code) is no longer available. Scientists that have tested my algorithm have found it useful to understanding their study species. My hope is that now that the growth function of Pauly et al. (1992) is available to more scientists that it will be considered in more situations, that the growth function will be rigorously tested against other seasonal growth functions, and that this increased use will increase our understanding of the seasonal growth of fishes.

I do not have any conflicts of interest or financial or material benefit interests related to the publication of this manuscript. I have followed the Guide to Authors and Submission Checklist found on your website.

Thank you for your consideration. We look forward to your response about the suitability of this note for publication in *Fisheries Research*. Please feel free to contact me if you have any questions or concerns related to this manuscript.

Respectfully,

Derek H Ogle

Dr. Derek H. Ogle
Professor of Mathematical Sciences and Natural Resources

***Highlights (for review)**

- The mathematical foundation of the seasonal cessation in growth model proposed by Pauly et al. (1992) is reviewed.
- An algorithm for implementing the seasonal cessation in growth model proposed by Pauly et al. (1992) in any software capable of performing nonlinear least-squares is proposed.
- Use of the algorithm is demonstrated with four sets of seasonal length-at-age data.

An Algorithm for the von Bertalanffy Seasonal Cessation in Growth Function of Pauly et al. (1992)

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Abstract

Pauly et al. (1992; Australian Journal of Marine and Freshwater Research 43:1151–1156) introduced a modified von Bertalanffy seasonal growth function that allowed for a period of no growth. Pauly et al. (1992) provided special purpose software to fit the model to length-at-age data but this software is no longer available and specific details to implement a critical aspect of the new growth function were not clear. I provide details for this critical aspect of the function, implement the function in the open-source R environment, and briefly demonstrate the use of this function with four data sets. With this, the growth function of Pauly et al. (1992) is now readily available to all scientists with access to software that can fit nonlinear models to data. Thus, this growth function may be implemented in more situations and its fit rigorously compared to the results from other models of seasonal fish growth.

Keywords: Growth, Seasonal, Cessation, Nonlinear Modeling

1. Introduction

The mean length-at-age for many fish (Haddon, 2011) and other aquatic animals (e.g., Hota, 1994; Harwood et al., 2014) is often modeled with the von Bertalanffy growth function (VBGF; von Bertalanffy, 1938). A common foundation for several parameterizations of the VBGF is

$$L_t = L_\infty(1 - e^{-q})$$

where L_t is the expected or average length at time (or age) t, L_∞ is the asymptotic mean length, and q is at least a function of t. For example, the most common parameterization of the VBGF attributable to Beverton and Holt (1957) uses

$$q = K(t - t_0) \quad (1)$$

where K is a measure of the exponential rate at which L_t approaches L_∞ (Schnute and Fournier 1980) and t_0 is the theoretical time or age at which L_t would be zero.

Many fish exhibit seasonal oscillations in growth as a response to seasonal changes in environmental factors such as temperature, light, and food supply (e.g., Bayley, 1988; Pauly et al., 1992; Bacon et al. 2005; Garcia-Berthou et al., 2012; Carmona-Catot et al., 2014). Various modifications of Equation 1 have been used to model these seasonal oscillations in growth. The most popular of these modifications, from Hoenig and Choudaray Hanumara (1982) and Somers (1988) with a clarification by Garcia-Berthou et al. (2012), uses

$$q = K(t - t_0) + S(t) - S(t_0) \quad (2)$$

with $S(t) = \frac{CK}{2\pi} sin(2\pi(t - t_s))$. In Equation 2, t_s is the time between time 0 and the start of the convex portion of the first sinusoidal growth oscillation (i.e., the inflection point) and C is the proportional decrease in growth at the depth of the growth oscillation (i.e., "winter"). Equation 2 may represent no seasonal oscillation in mean length (C=0) or a reduced but not stopped increase in mean length (for 0<C<1), a complete stop in the increase in mean length (C=1), and a decrease in mean length (C>1) during the "winter" (Figure 1). The point where the increase in mean length is smallest is called the "winter-point" (WP) and is at $t_s + \frac{1}{2}$ because the sine function in Equation 2 has a period (i.e., the growth period) of one year.

Pauly et al. (1992) argued that a decrease in mean length with increasing age is unlikely for organisms whose skeletons largely preclude shrinkage and, thus, values of C>1 from Equation 2 were unrealistic for length (but not weight) data. Pauly et al. (1992) then proposed a modification to Equation 2 that included a no-growth period where mean length was not allowed to decrease. Specifically, their modification is

$$q = K'(t' - t_0) + V(t') - V(t_0) \tag{3}$$

with $V(\mathrm{t}) = \frac{K'(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(\mathrm{t} - t_s)\right)$. In Equation 3, NGT is the "no-growth time" or the length of the no growth period (as a fraction of a year) and t' is found by "subtracting from the real age (t) the total no-growth time occurring up to age t" (Pauly et al. 1992). Furthermore, because the units of K changed from $year^{-1}$ in Equation 2 to $(1 - NGT)^{-1}$ in Equation 3, Pauly et al. (1992) suggested using K' in Equation 3 to minimize confusion with K from Equation 2.

Pauly et al. (1992) devised Equation 3 by assuming C=1 and replacing 2π in Equation 2 with $\frac{2\pi}{1-NGT}$ (i.e., restricting the seasonal oscillation to the growth period and noting that K' only operates during the growth period). Their modification may be described geometrically (though not algorithmically) in two steps. First, Equation 2 with (fixed) C=1 is fit to the observed lengths and ages that have had the cumulative NGT subtracted (i.e., using t'). This growth trajectory is then separated at each WP and horizontal segments that are NGT units long are inserted at these points. This forms a growth trajectory that smoothly transitions into and out of the no-growth periods (Figure 2).

Pauly et al. (1992) provided a then ubiquitous but now obsolete 3.5-in "diskette" with a computer program to estimate the parameters of Equation 3; however, the last diskette has been lost and the source code is no longer available (D. Pauly, pers. comm.). Pauly et al. (1992) did describe the operations performed by their program, but there is no detailed description of how t' should be operationalized. This is an important step in using Equation 3 because t' is a function of t, but it is also a function of NGT and t_s, which are parameters to be estimated during the model-fitting process. Thus, the values for t' change with each iteration of the non-linear model-fitting algorithm.

Therefore, the objectives of this note are to (i) operationalize the calculation of t', (ii) provide an (open-source) algorithm for the calculation of t' and Equation 3 for use in model fitting, and (iii) illustrate the use of this algorithm.

2. Methods

The algorithm developed to fit Equation 3 is demonstrated with four data sets. The first data set is the fork lengths (mm) and decimal ages (the number of opaque zones observed on otolith thin sections plus the proportion of the year after the designated birthdate) from 215 Australian bonito (*Sarda australis*) sampled from commercial landings as detailed in Stewart et al. (2013). Stewart et al. (2013) fit Equation 2 to these data but constrained C to not exceed 1. These data were chosen to illustrate how Equation 3 may provide a better and more appropriate fit then Equation 2 with the boundary condition of $C = 1$. The remaining three data sets are for invasive Eastern mosquitofish (*Gambusia holbrooki*) from southern France to southern Spain detailed by Carmona-Catot et al. (2014). Standard lengths (mm) were measured for each fish and annual ages were estimated from length frequencies and analysis of scales, with decimal ages determined from capture date and estimated birth dates for a cohort. Carmona-Catot et al. (2014) fit Equation 2, without constraining C, to fish from ten locations. Data from three locations were chosen to be examined here to demonstrate how Equation 3 fits relative to Equation 2 with varying estimates of C (i.e., site 2 had C much greater than 1, site 4 had C only slightly greater than 1, and Site 9 had C much less than 1).

We used the "port" algorithm in the nls() function in R (R Development Core Team 2016) to estimate the parameters for both Equations 2 and 3 for all four data sets. Starting values for L_∞, K, and t_0 were obtained from the vbStarts() function in the FSA package v0.8.8 (Ogle 2016b) as described in Ogle (2016a). Starting values for t_s, C and NGT were obtained by visual examination of the length versus age plot. Starting values for K' were derived from the starting value for K divided by 1 minus the starting value for NGT. Values of L_∞, K, and K' were constrained to be positive, t_s and NGT were constrained to be between 0 and 1, and C was constrained to be between 0 and 1 for the Australian bonito data and positive for the mosquitofish data. The growth function with the lowest Akaike Information Criterion (AIC) value was chosen as the better fit for each data set. Confidence intervals for each parameter were the 2.5% and 97.5% percentile values of non-parametric bootstrap parameter estimates computed with the nlsBoot() function from the nlstools package v1.0-2 (Baty et al. 2015) in R.

3. Results

3.1 Calculating t'

As noted by Pauly et al. (1992) the calculation of t' depends on the observed age (t) and the cumulative no-growth time prior to t. In practice, the calculation of t' also depends on the position of the no-growth period within a year. Here, the position of the no-growth period is defined relative to WP and NGT, such that the following algorithm may be used to convert from observed ages (t) to ages adjusted for cumulative NGT prior to age t (t'). With this, t' may be calculated with the following six steps.

1. Shift the age (t) by subtracting the start of the no-growth (SNG) period (i.e., $SNG = WP - \frac{NGT}{2} = t_s + \frac{1}{2} - \frac{NGT}{2}$; Chatzinikolaou and Richardson 2008) from t, such that a whole number will represent the start of a no-growth period. For example, if SNG=0.4, then t=2.4 will become 2.0 and t=2.9 will become 2.5.
2. Subtract the whole number age (i.e., fully completed growth years) from the shifted age from Step 1 such that the remaining decimal represents the fraction of a shifted year. For example, a 0 will result if the shifted age is 2.0 and a 0.5 will result if the shifted age is 2.5.
3. Substract the NGT from the value from the previous step.
4. If the value from the previous step is negative, then the age is within the no-growth period and the negative value should be replaced with a zero. Otherwise, the positive value represents the amount of time into a growth period.
5. Add the value from the previous step to the total growth time completed (i.e., the product of the number of growth periods completed and the length of the growth period ($1 - NGT$)).
6. Compute t' by adding back the SNG that was subtracted in Step 1.

Further examples of t' values relative to t values are shown in Figure 2. This algorithm for computing t' is implemented in an R (R Development Core Team 2016) function as shown in

Appendix 1. With this, Equation 3 is easily implemented as an R function as shown in Appendix 2. For convenience, Equation 3 is implemented in the vbFuns() function of the FSA package (Ogle 2016b).

3.1 Examples of Fitting the Function

Equation 3 fit the Australian bonito data slightly better (a lower AIC value; Table 1) than Equation 2. The length of the no-growth period was estimated to be 0.13 or 13% of the year. The t_s parameters were equal and the L_∞ parameters were similar, but the t_0 parameters differed somewhat between the two functions (Table 1). Graphically, there was little perceptual difference in the fits of the two growth functions (Figure 3A).

Equation 3 did not fit the mosquitofish data better in situations where there was some evidence for a decrease in mean length with increasing age (i.e., C>>1 in Equation 2; e.g., Site 2; Table 1; Figure 3B) or no evidence for a cessation in growth (i.e., C<1 in Equation 2; e.g. Site 9; Table 1; Figure 3D). However, Equation 2 appeared to respond too dramatically to one sample of ages (approx. 0.4) at Site 2, and Equation 3 likely provides more realistic estimates of mean length throughout the seasonal cessation in growth period in this example (Figure 3B). Equation 3 fit better than Equation 2 when a cessation in growth was evident without an apparent decline in mean length with age for mosquitofish (i.e., Site 4; Table 1; Figure 3C).

4. Discussion

Pauly et al. (1992) introduced a novel function for modeling the seasonal cessation in growth in length of fishes. The growth function proposed by Pauly et al. (1992) incorporates only cyclic seasonal effects (Wang and Jackson 2000) and, thus, assumes that t_s, or equivalently WP or

SNG, occurs at the same time each year (or at each age), that the NGT is greater than 0 and, if so, is the same length each year(or at each age) , and that the mean length does not decrease over time. These are stringent assumptions that are likely not appropriate for all species, locations, and times. Thus, Equation 3 is very likely not the globally best seasonal growth model, as illustrated here with the mosquitofish examples.

The growth function in Pauly et al. (1992) does not appear to have been widely used. Pauly et al. (1992) has been cited at least 70 times (from Google Scholar and ResearchGate searches on 31-May-16); though it appears that only two of 43 journal (excludes citations in books, dissertations, reports, other non-journal citations, and journals not published in English) actually fit Equation 3 to data. Of these, Chatzinikolaou and Richardson (2008) used the special purpose LFDA software (www.mrag.co.uk/resources/lfda-version-50) to fit Equation 3 to length frequency data, whereas it is not clear how Beguer et al. (2011) fit the function, though they did fix L_∞ to a constant value.

Perhaps the growth function of Pauly et al. (1992) has not been widely adopted because it is not clear how to actually fit the function to length-at-age data. Alternatively, it may be that this function does not adequately represent seasonal growth trajectories, though we are unaware of any rigorous comparison between Equation 3 and other seasonal growth models. The carefully described algorithm and R function provided here for computing t', which allows for Equation 3 to be statistically fit to seasonal age data, appears to provide reasonable parameter estimates for the four examples provided. Thus, the Pauly et al. (1992) growth function is now available to all scientists with access to software (e.g., R) that can fit nonlinear models to data. Thus, with the methods presented in this note, Equation 3 can now be implemented in more situations and its fit rigorously compared to the results from other models.

Acknowledgments

John Stewart (New South Wales Department of Primary Industries Fisheries) graciously provided the Bonito length-at-age data. Emili Garcia-Berthou (Universitat de Girona) kindly provided the mosquitofish length-at-age data. This paper was improved by discussions with and reviews by Emili Garcia-Berthou, Andrew Jensen, and Danial Pauly. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Appendix A. R Function to Compute t'

```
#################################################################
## internal function to compute t-prime
#################################################################
iCalc_tpr <- function(t,ts,NGT) {
  ## Step 1
  SNG <- ts+(1-NGT)/2
  tmp.t <- t-SNG
  ## Step 2 (in parentheses) and Step 3
  tmp.t2 <- (tmp.t-floor(tmp.t))-NGT
  ## Step 4
  tmp.t2[tmp.t2<0] <- 0
  ## Step 5 (in parentheses) and Step 6 (also returns value)
  (floor(tmp.t)*(1-NGT)+tmp.t2) + SNG
}
```

Appendix B. R Function for Equation 3 (Pauly et al. (1992) Function)

```
#################################################################
## Main Function
##   Linf, t0 as usual
##   Kpr = K-prime as defined in Pauly et al. (1992)
##         (units are different than usual K)
##   ts = start of sinusoidal growth (maximum growth rate)
##   NGT = "No Growth Time" = "fraction of a year where no
```

```
##          growth occurs"
##   tpr = "t-prime" = age (t) minus cumulative NGT prior to t
#################################################################

vbSCGF <- function(t,Linf,Kpr=NULL,t0=NULL,ts=NULL,NGT=NULL) {
  ## Allow parameters to be sent as one vector in Linf
  if (length(Linf)==5) { Kpr <- Linf[[2]]; t0 <- Linf[[3]]
  ts <- Linf[[4]]; NGT <- Linf[[5]]
  Linf <- Linf[[1]] }
  ## Adjust ages for NGT (i.e., compute t-prime)
  tpr <- iCalc_tpr(t,ts,NGT)
  ## Equation 3 (i.e., Pauly et al. (1992) growth function)
  q <- Kpr*(tpr-t0) +
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(tpr-ts)) -
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(t0-ts))
  Linf*(1-exp(-q))
}
```

Online Supplement

R code for all figures and analyses.

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Table 1. Parameter estimates and Akaike Information Criterion (AIC) values from the fits of Equation 2 and Equation 3 to the Australian bonito and three sites of Eastern mosquitofish data. The lower AIC between the two equations for the same dataset is boldfaced.

Equation 2 (Somers (1988) function)					Equation 3 (Pauly et al. (1992) function)				
	Australian Bonito	Mosquitofish				Australian bonito	Mosquitofish		
		Site 2	Site 4	Site 9			Site 2	Site 4	Site 9
L_∞	71.9	35.9	46.0	41.6	L_∞	71.7	35.1	44.0	47.0
	(59.6,125.8)	(34.5,37.6)	(40.1,56.2)	(39.1,44.9)		(58.5,124.7)	(33.8,36.8)	(38.9,57.6)	(42.4,57.0)
K	0.27	2.01	1.05	1.31	K'	0.31	4.64	1.60	0.77
	(0.09,0.46)	(1.68,2.35)	(0.63,1.57)	(1.00,1.71)		(0.10,0.76)	(3.25,6.70)	(0.85,2.58)	(0.51,1.12)
t_0	-1.9	-0.02	-0.20	-0.21	t_0	-1.6	0.43	0.07	-0.41
	(-3.0,-1.2)	(-0.04,-0.01)	(-0.28,-0.14)	(-0.30,-0.15)		(-2.8,-0.7)	(0.35,0.50)	(-0.04,0.18)	(-0.49,-0.19)
t_s	0.09	0.88	0.75	0.72	t_s	0.09	0.92	0.76	0.61
	(0.00,0.19)	(0.87,0.89)	(0.72,0.78)	(0.66,0.76)		(0.00,0.17)	(0.91,0.93)	(0.69,0.79)	(0.55,0.65)
C	1.00[a]	1.95	1.28	0.62	NGT	0.13	0.43	0.26	0.00
	(0.44,1.00)	(1.82,2.05)	(1.13,1.44)	(0.46,0.80)		(0.00,0.49)	(0.37,0.48)	(0.16,0.45)	(0.00,0.26)
AIC	1435.9	**4159.4**	4070.6	**4995.8**	AIC	**1435.4**	4175.4	**4059.9**	5018.4

[a] C was constrained to be less than or equal to 1 during model fitting.

Figure Labels

Figure 1. Example VBGF using Equation 2 with L_∞=30, K=0.3, t_0=-0.1, t_s=0.05 (with WP=0.55) and four different values of C.

Figure 2. Example VBGF using Equation 3 with L_∞=30, K'=0.35, t_0=-0.1, NGT=0.3, and t_s=0.05 (with WP=0.55). Each t_s is shown by a gray point, WP by a vertical arrow, and no-growth period by the horizontal interval centered on the WP arrow and the gray region that extends to the x-axis. The ages adjusted for the NGT (i.e., t') are shown above the x-axis.

Figure 3. Fork lengths at age for Australian Bonito (A) and standard lengths at age for Eastern mosquitofish at Sites 2 (B), 4 (C), and 9 (D) with the best-fits of Equation 3 (black line) and Equation 2 (gray line) superimposed. Parameter estimates (and 95% confidence intervals) from the model fits are shown in Table 1.

Figure 1

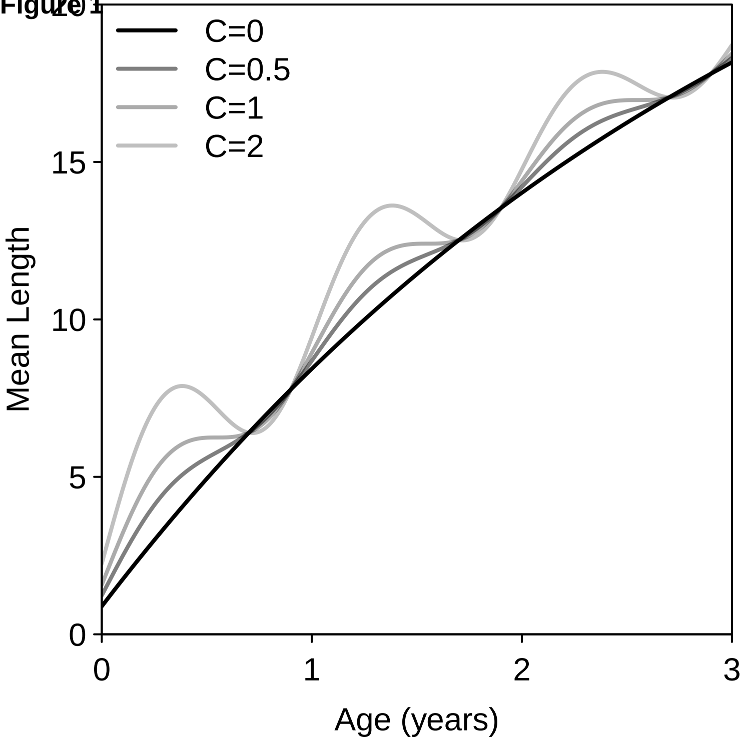


Figure 2

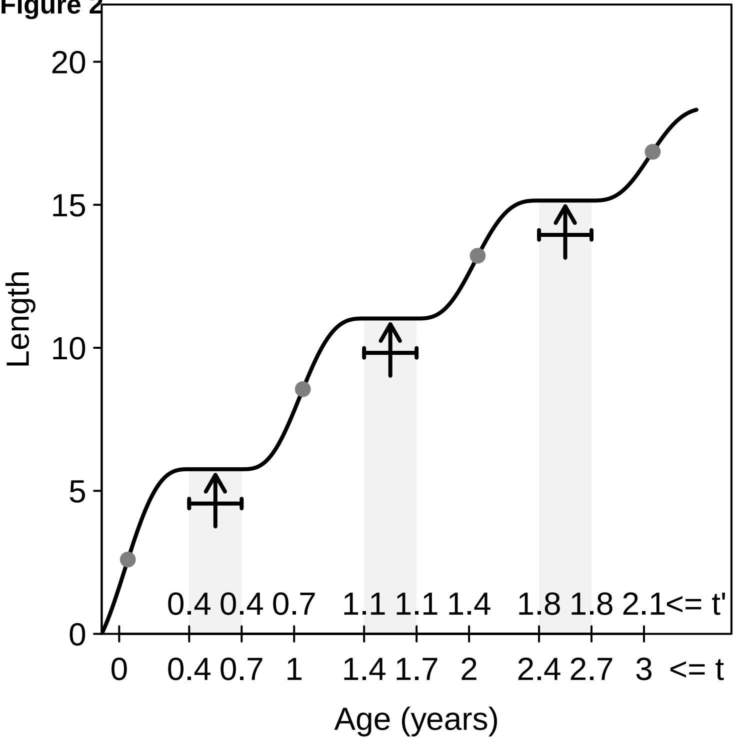
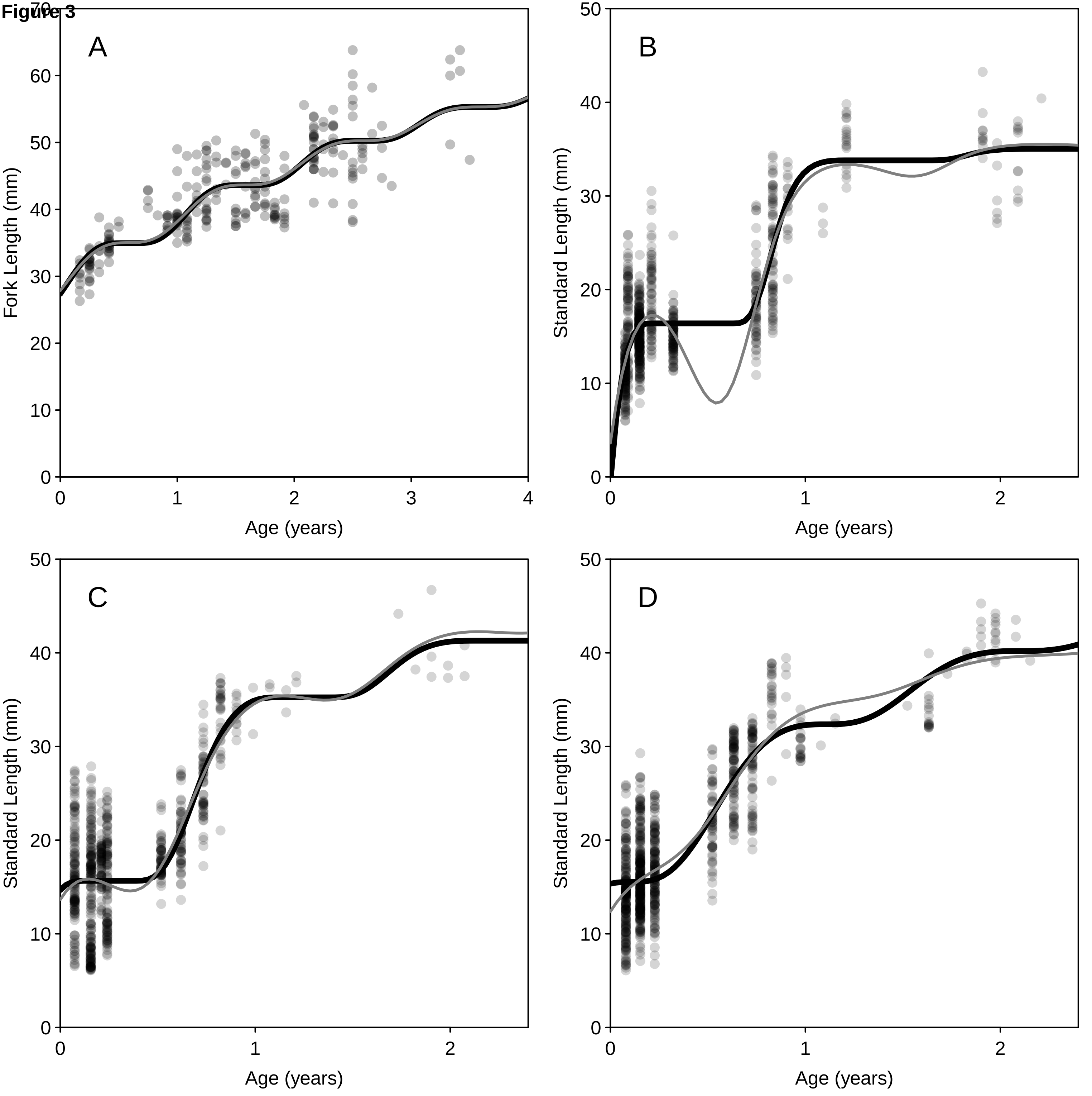

20
15
10
5
0
Length
0.4 0.4 0.7 1.1 1.1 1.4 1.8 1.8 2.1 <= t'
0 0.4 0.7 1 1.4 1.7 2 2.4 2.7 3 <= t
Age (years)

Figure 3


A
Fork Length (mm)
70
60
50
40
30
20
10
0
0
1
2
3
4
Age (years)
B
Standard Length (mm)
50
40
30
20
10
0
0
1
2
Age (years)
C
Standard Length (mm)
50
40
30
20
10
0
0
1
2
Age (years)
D
Standard Length (mm)
50
40
30
20
10
0
0
1
2
Age (years)